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A Space-For-Time approach to study the effects of increasing temperature on leaf litter decomposition under natural conditions

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ABSTRACT

Decomposition processes influence the formation of soil organic carbon stocks, and it is necessary to understand how both will respond to climate change. A Space-For-Time (SFT) substitution allows the comparison of litter decomposition under current and future conditions in the field, using a spatial gradient of environmental conditions. Here we used a SFT approach to study the effects of a difference in temperature similar to the predicted increase of 3.2–3.5 °C in Central Europe until 2100. To simulate this difference, we setup a five-fold replicated SFT substitution along mountain slopes and compared decomposition in two sites differing in ∿3.6 °C (600 *vs* 1200 m a.s.l). With this setup we compared the decomposition of high-quality (nettle) and low-quality (hay) litter, with and without fauna access, during summer, in five mountains in the Austrian Alps (Salzburg). Temperature loggers placed in one of the mountains indicated that the actual difference between the two altitudes was only ∿1.8 °C during summer. Nonetheless, decomposition of low-quality litter was 12% faster at 600 m than at 1200 m; altitude alone explained 19% of total variance. On the contrary, decomposition of high-quality litter was 9% faster at 1200 m. Fauna was the main driver of the high-quality litter decomposition at both altitudes and explained 26% of total variance, whereas altitude explained only 10%. Decomposition rates of the high-quality litter ($21.4 \pm 2.9\,mg\,g^{-1}\,d^{-1}$; ± s.d.) was much higher than that of the low-quality ($7.9 \pm 1.0\,mg\,g^{-1}\,d^{-1}$). Overall, the decomposition of the low-quality, slow-decomposing litter was more sensitive to warming and less influenced by the activity of detritivores, compared to a litter of higher quality. Through the use of the SFT substitution, we detected that a large part of the variance explained by the models was due to the variability between blocks and mountains, highlighting the important effect of spatial heterogeneity and the need for more replicated, field-based studies, to estimate the responses of decomposition processes to climate change.

1. Introduction

Soil carbon stocks are mainly driven by the interplay between the input of organic matter and its decomposition and decay rates. In temperate forests, litterfall provides the main input of organic matter, and it is the source of 70–80% of the total soil carbon (Liski et al., 2002). Litter decomposition rates are mediated by the interaction of climate, activity of detritivores and decomposers, and litter quality (Melillo et al., 1982; Aerts, 1997; Trofymow et al., 2002; Hättenschwiler and Gasser, 2005; Cotrufo et al., 2013). Litter quality, i.e. its chemical composition upon decomposition (Melillo et al., 1982), is usually indicated by traits such as nitrogen and lignin content, C:N ratio, toughness, and phenolic compounds (Melillo et al., 1982; Zhang et al., 2008). Earlier and recent studies have repeatedly demonstrated the control of nitrogen and lignin over decomposition rates (Mentemeyer, 1978; Aber et al., 1990; Preston and Trofymow, 2000; Cornelissen et al., 2004; Zhang et al., 2008), and lately the importance of other factors, such as water saturation capacity, magnesium (Makkonen et al., 2012), and calcium (García-Palacios et al., 2016) have also been shown. The traits that determine litter quality also determine decomposability (Zhang et al., 2008), digestibility (Cornelissen et al., 2004) and palatability to detritivores (Quadros et al., 2014). Detritivores, in turn, increase decomposition rates by processing the litter and producing a more easily degradable substrate (Wolters, 2000; Zimmer, 2002) and/or favouring the activity of microorganisms along the passage through the gut (Zimmer and Topp, 1998). Ultimately, climate, mainly temperature and precipitation, modulates both the activity of detritivores and microorganisms (Wall et al., 2008; García-

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Palacios et al., 2013) and the physical degradation of litter through UV degradation and drying-rewetting cycles.

Compared to forests of warmer regions, European cold temperate forests usually have the following combination of conditions: shorter growing seasons, lower abundance and/or activity of detritivores and microorganisms due to low temperatures, and abundant tree species that produce low-quality, lignin-rich and nutrient-poor litter (such as beech, spruce, and pine litter; Hättenschwiler and Gasser, 2005; Vesterdal et al., 2008). In combination, these conditions favour low litter decomposition rates and the stabilization and accumulation of carbon in the topsoil. For instance, there is a positive relationship between the total carbon in the forest floor and the C:N ratio of the leaf litter, a high C:N usually indicating low-quality litter (Vesterdal et al., 2008). It is not surprising, thus, that soils of old-grown temperate forests hold important carbon sinks (Luyssaert et al., 2008; Zhu et al., 2015). For the last two decades there has been an increasing concern about the stability of such soil carbon stocks upon climate change, and especially upon temperature increase (Goodale et al., 2002; Cornelissen et al., 2007; Luyssaert et al., 2008; Hagedorn et al., 2010b; Sarmiento et al., 2010). The average annual temperature in Europe is predicted to increase by 1–4 °C (B2 scenario) or 2.5–5.5 °C (A2 scenario) until 2100 (Christensen et al., 2007), and, due to the sensitivity of decomposition to temperature, increased temperatures can turn soil sinks into sources of CO_2 if decomposition rates increase (Davidson and Janssens, 2006; Hagedorn et al., 2010b; Spohn, 2015). Litter quality plays an important role in mediating these effects because the magnitude of temperature sensitivity depends on substrate quality ("carbon quality-temperature hypothesis"; Bosatta and Ågren, 1999; Fierer et al., 2005), increasing with decreasing litter quality. Low-quality substrates should have higher sensitivity to temperature because of a higher number of steps needed for its decomposition (Bosatta and Ågren, 1999). Coupled to that, relative more microbial CO_2 is produced (Spohn, 2015).

The effects of environmental changes on litter decomposition rates have been studied mainly under controlled conditions in microcosm experiments in the laboratory (Petchey et al., 1999; Hättenschwiler and Bretscher, 2001; Rouifed et al., 2010). Alternatively, there's the experimental manipulation of abiotic variables in the field (Luo et al., 2001; Dang et al., 2009), such as the warming of top soil layers using wires (Hagedorn et al., 2010a). Here we employed a third approach, the Space-For-Time (SFT) substitution (Pickett, 1989; Fukami and Wardle, 2005). The idea of SFT is to identify natural gradients, therefore "the space", representing two or more contrasting conditions that represent current and future scenarios, therefore "the time" (Pickett, 1989). Our SFT approach to study the effects of temperature increase used the natural environmental gradients of mountain slopes. Altitudinal gradients provide an excellent opportunity for addressing abiotic effects on ecological processes under field conditions: some abiotic factors change in a predictable way with increasing altitude, while biotic factors, such as fauna and plant communities, remain similar, at least within altitudinal ecotones (e.g. montane, alpine, nival) (Aerts, 2006). Temperature, for instance, is expected to decrease with increasing altitude, making *"Latitudinal and altitudinal gradients […] natural, long-term analogues for climate change"* (Aerts, 2006): air temperature decrease (or adiabatic rate) is, on average, 0.6 °C per 100 m elevation, with a range of 0.2–0.8 °C per 100 m (Nagy and Grabherr, 2009). Having this rate in mind, we used an altitudinal difference of 600 m, within the lower montane belt, to obtain a temperature difference of ∿3.6 °C between sites, attempting to simulate the predicted temperature increase in Central Europe (Christensen et al., 2007). Our aim was to quantify the effects of this small difference in temperature on litter decomposition rates in the field, but considering also the interactions between litter quality, soil fauna and microorganisms. Due to the know sensitivity of decomposition to temperature (Fierer et al., 2005) and according to previous studies along altitudinal gradients (Shanks and Olson, 1961; Coûteaux et al., 2002; Wang et al., 2010), we predicted that decomposition rates would be higher at the lower altitude (higher average temperature). Due to the expected decrease in abundance of soil fauna with increase in altitude (Hoover and Crossley, 1995; Wang et al., 2009), and to their known preference for high-quality litter (Quadros et al., 2014) and higher effects on its decomposition (Rouifed et al., 2010), we predicted that faunal effects would be stronger at the lower altitude and on the high-quality litter. We chose two litter types of contrasting quality and manipulated the fauna access into the mesocosms using different mesh sizes. We replicated the study on five closely situated mountains to account for the effects of habitat spatial heterogeneity and provide a realistic estimation of effects of temperature increase on litter decomposition rates.

2. Methods

2.1. Study sites

In order to find appropriate mountains to replicate our study, we analysed hiking track maps of the vicinities of Salzburg, Austria, searching for mountains that had 1) an accessible north slope; 2) minimum elevation of 1200 m; 3) forests dominated by *Fagus sylvatica* with the presence of *Picea abies*. Through this search, and based on previous personal experience, we chose five mountains: Gaisberg (47°48′N, 13°06′W; 1287 m), Untersberg (47°41′N, 12°59′W; 1973 m), Tristkopf (47°32′N, 13°07′W; 2110 m), Wirreck (47°34′N, 13°12′W; 1473 m), and Kleiner Göll (47°35′N, 13°07′W; 1752 m). The soil types are Calcaric Leptosols (WRB classification; IUSS Working Group WRB, 2015). Besides *Fagus sylvatica* and *Picea abies*, other woody trees in these mountains were *Abies alba*, *Acer platanoides*, *Acer pseudoplatanus*, *Fraxinus excelsior*, and *Ulmus glabra*. A more detailed list of species can be seen in Schwap et al. (2000). The most common macrodetritivores seen in our study sites were diplopods *Glomeris pustulata* (Fabricius, 1781) and *Cylindroiulus* spp., woodlice *Armadillidium versicolor (Stein 1859), Trachelipus rathkii* (Brandt, 1833), *T. ratzeburgii* (Brandt, 1833), and land snails.

On each mountain we established two sites, one at 600 m a.s.l. and another at 1200 m a.s.l., totalling 10 sites (Fig. 1). Exceptionally, due to difficult access, on Untersberg the lower site was located at 750 m a.s.l. and the upper one at 1240 m a.s.l. According to the classification of Körner et al. (2011), both the 600 m and 1200 m sites belong to the Lower Montane thermal belt, a mountain thermal zone characterized by growing seasons with mean temperatures between 10 and 15 °C. To estimate the actual mean air temperature (at the soil surface) during the field study, we placed temperature loggers (HOBO) at 450, 750, 1040 and 1240 m a.s.l. along one of the five altitudinal transects (Untersberg,

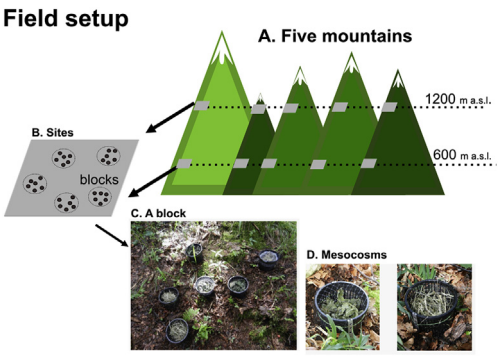

Fig. 1. Schematic representation of the field setup. A) We chose five mountains, in the surrounding of Salzburg, Austria, ranging from 1287 to 2110 m altitude; B) Along the northern slopes we stablished one site at 600 m a. s. l. and one at 1200 m a. s. l. (except for Untersberg, see text), totaling 10 sites; C) Each site had five blocks. Each block had six mesocosms (i. e. three types of mesocosms for different faunal access for each litter type), with 300 in total; D) Examples of mesocosms with high-quality litter (*Urtica dioica* leaves) in the left, and low-quality litter (hay leaves), in the right.

Table 1
Properties of the two leaf litter types used in this study, high-quality (*Urtica dioica*) and low-quality (hay). Total N and C:N were obtained in a C:N analyzer (n = 3); total phenolics (tannic acid equivalents) were obtained with the Folin-Ciocalteau assay (n = 7). Values are means ± standard deviation. The P value indicates the result of a T-test between the two litter types.

	High-quality	Low-quality	P
Total nitrogen (%)	3.6 ± 0.4	1.7 ± 0.2	0.002
C:N	9.8 ± 0.4	24.3 ± 1.2	< 0.001
Total phenolics	0.62 ± 0.01	0.80 ± 0.03	< 0.05

Salzburg).

2.2. Leaf litter

We compared two litter types of contrasting quality, mixed hay (grass) and the stinging nettle *Urtica dioica*. Hay is a nitrogen-poor, lignin-rich litter. Hay was purchased in a local store, and stems, roots and flowers were manually sorted out to obtain a batch with only leaf litter. We used *U. dioica* leaves as a high-quality litter, which is nitrogen-rich and has very soft leaves. *Urtica* litter was obtained by cutting green leaves and air-drying them for seven days. To further characterize our leaf litter batches, we measured total phenolics (an indicator of deterrent compounds) with the Folin-Ciocalteau assay following the protocol of Bärlocher and Graça (2005), and the total nitrogen and organic carbon (C:N ratio) with a CN analyser. As expected, there was a large difference in N, and C:N ratio between these two litter types, which is consistent with previous studies (4.5% N for nettle and 0.7% for grass; see Lehtomäki et al., 2008) (Table 1).

2.3. Field set-up

Field mesocosms for quantifying litter decomposition rates were made of plastic flower pots (Fig. 1). To manipulate the access of mesofauna and/or macrofauna we made a few changes to the pots. They had 2 × 2 mm holes, which allowed the access by mesofauna. To further allow the access by macrofauna and create the macrofauna + mesofauna treatment, we drilled additional 10 × 6 mm holes on the sides. To estimate the effect of microorganisms-only (control treatment), we prevented the access of both mesofauna and macrofauna, by covering the inner side of the pots with a soft cotton fabric (0.2 × 0.2 mm mesh size). The same fabric was used to seal the bottom of all pots to avoid the access of the fauna from the bottom, while allowing for water drainage. Each mesocosm received ~5 g of one litter type, previously dried (48 h at 35 °C) and weighed. The top of each mesocosm was covered with a 10 × 10 mm mesh, to prevent the addition of foreign material. All mesocosms were fixed to the soil with metal pins, disposed in blocks of six (2 litter types x 3 fauna treatments), with five blocks per altitude and per site. In total, 60 mesocosms were placed on each mountain, with 300 overall (2 litter types x 3 fauna treatments x 5 blocks x 2 altitudes x 5 mountains) (Fig. 1). Mesocosms within a block where placed 15–30 cm away from each other, and the distance between blocks was 3–5 m. The block design intended to account for the possible effects of the high terrain heterogeneity (litter cover, soil depth, exposed rocks, inclination, etc.) observed along the mountain slopes and between mountains.

The mesocosms were installed in the field in July 2012. Initially, we planned to run the experiment until the end of summer, however, one month after the beginning of the experiment, we visited one of the sites and noticed that more than half of the high-quality litter had been lost, while the low-quality changed little. Thus, we recollected the mesocosms with high-quality litter after 36–41 days in the field, whereas the low-quality was recovered after 60–83 days in the field. The installation and removal dates varied from mountain to mountain depending on weather conditions, and only one mountain was visited per day. Two mesocosms were lost. In the laboratory, the remaining litter was dried (48 h at 35 °C) and weighed to yield the mass loss.

2.3.1. Analyses

All statistics were performed using R (R Core Team., 2017) and RStudio®. For the air temperature data, collected hourly during our field study (July–September 2012), we calculated the daily mean, maximum, and minimum values at each altitude. Linear models were then used to calculate the relationship between temperature and altitude.

Litter decomposition rates were calculated as mg day^{-1} (dry weight) to account for differences in the duration of the experiment between mountains and litter types. To facilitate comparisons with other litter decomposition studies we also show the data as mg g^{-1} day^{-1} (dry weight). We used a linear mixed-model to investigate the effects of altitude and fauna, both serving as fixed effects, on litter decomposition rates. We considered the blocks nested within sites as random effects. We started all analyses with a null model that included only the random factors; we added the fixed factors and the interaction terms to this model one by one and checked whether the model was improved. Model fit was assessed using chi-square tests on the log-likelihood of different models. These analyses were done with the packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017). The marginal and conditional effects sizes, proposed by Nakagawa and Schielzeth (2013), were calculated for the best model using piecewiseSEM (Lefcheck and Frecketon, 2016). The mixed-models were applied to the high- and low-quality litter separately, as we were not interested in differences between them *per se*. The low-quality data was log-transformed prior the calculation of the final models, as the inspection of residuals with Shapiro's test indicated they were not homoscedastic. This transformation was not necessary for the high-quality litter.

3. Results

3.1. Air temperature at the soil surface

As expected, the mean, minimum, and maximum air temperature decreased linearly with altitude (Fig. 2). During the field experiment, the mean temperature at soil surface was described by the equation T (°C) = −0.0031 altitude (m) +16.4908 ($F_{1;10}$ = 3.893, p = 0.07). Based on this equation, the overall mean daily temperature was 14.6 °C at 600 m and 12.8 °C at 1200 m. Thus, the observed adiabatic rate of the soil surface temperature, in this mountain and period, was 3.1 °C km^{-1}, or 0.31 °C per 100 m. Hence, instead of having the 3.6 °C temperature

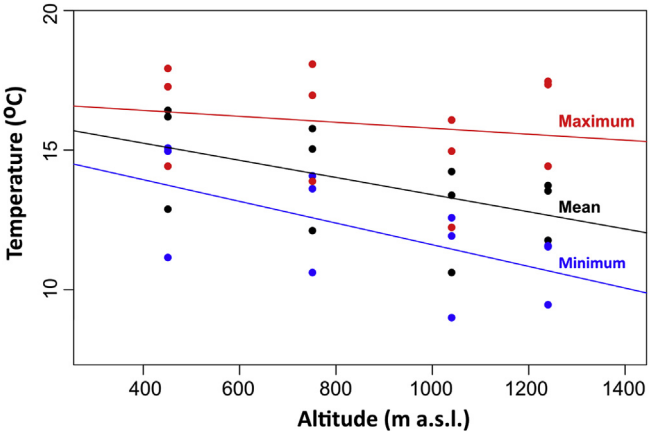

Fig. 2. Daily means of mean, maximum, and minimum air temperatures at the soil surface in Untersberg, Salzburg, Austria, during our field experiment (July–September 2012). Points represent daily means for July, August, and September calculated separately. Temperature loggers were placed at 450, 750, 1040, and 1240 m a.s.l.

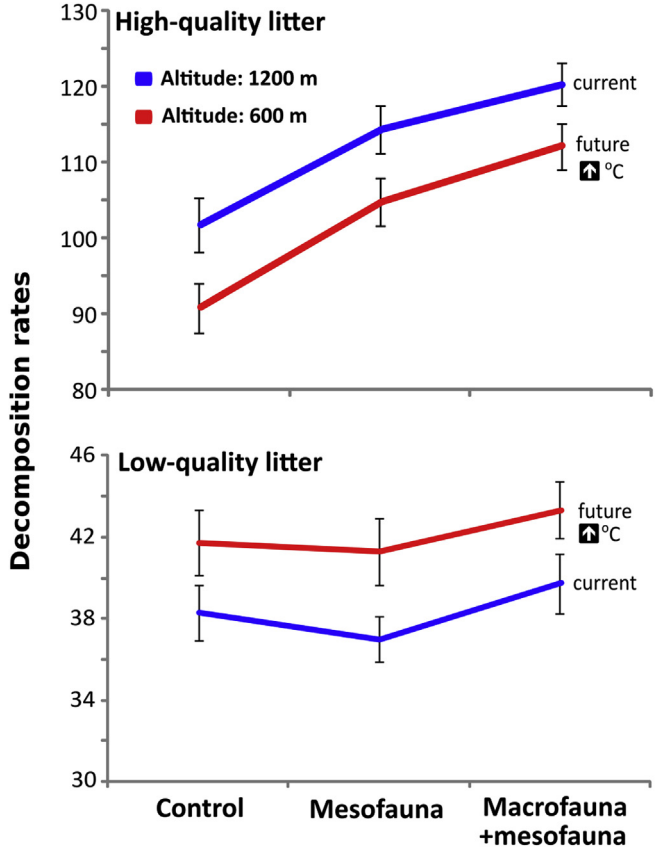

Fig. 3. Decomposition rates (mg day^{-1} ± s. e.) of high-quality (*Urtica dioica*) and low-quality (hay) and leaf litter, depending on altitude and fauna access. The litter was left to decompose in summer, during July–September 2012, in five mountains in Salzburg, Austria. The mean temperature at the 600 m sites was expected to be 3.6 °C higher than at 1200 m and the two altitudes were used to represent current (1200 m a.s.l.) and predicted future (600 m a.s.l.) scenarios of global warming for Europe. The means represent the data pooled across blocks (n = 5 per altitude and mountain).

difference between 600 and 1200 m a.s.l. we aimed at, we actually compared decomposition processes between sites with a mean temperature difference of 1.8 °C.

3.2. Litter decomposition rates

As expected, the high-quality litter decomposed much faster than the low-quality litter, regardless of fauna or altitude (Fig. 3). The high-quality litter decomposed 8.7% faster at 1200 m: mass loss rates were 112 ± 1.4 mg d^{-1} (22.3 ± 0.3 mg g^{-1} d^{-1}) at 1200 m and 104 ± 1.7 (20.5 ± 0.3 mg g^{-1} d^{-1}) at 600 m. Nonetheless, altitude (as a proxy for temperature) explained only 10% of the total variance (Table 2). However, fauna effects on the high-quality litter were evident, slightly higher at 600 m, and explained 26% of the total variance explained by the model (Table 2). Access by the fauna increased decomposition by 23% (at 600 m) and 18% (at 1200 m), relative to the controls. The mesofauna effect, relative to the controls, was 15% increase at 600 m and 12% increase at 1200 m. The macrofauna effect, calculated here as the difference between macrofauna + mesofauna treatment minus the mesofauna treatment, was 7% at 600 m and 5% at 1200 m (see coefficients in Table 3). The best minimum model for the high-quality litter had both altitude and fauna as significant fixed factors (Table 2). Together they explained 36% of the variance explained by the model, which was 71% (Table 2).

The low-quality litter decomposed 12% faster at 600 m than at 1200 m (42 ± 1 versus 38 ± 1 mg d^{-1}, or 8.4 versus 7.5 mg g^{-1} d^{-1}) (Fig. 3). The best minimum model had only altitude as a significant fixed factor, which explained 19% of total variance explained by the model. Thus, neither mesofauna nor macrofauna + mesofauna access affected the decomposition rates of low-quality litter, as compared to the controls. The coefficients of the models are shown in Table 3.

The random factors of the linear-mixed models used here expressed the importance of spatial heterogeneity, and they explained a significant proportion of the total variance: 36% (high-quality litter) and 45% (low-quality litter). In the case of high-quality litter this was mostly due to a high between-mountain variation leading to idiosyncratic effects of altitude on decomposition rates (Table 4): decomposition rates were higher at 1200 m only at Gaisberg, Kleiner Göll, and Untersberg, equal at Wirreck, and lower at Tristkopf. In the case of the low-quality litter, decomposition rates were always higher at 600 m than at 1200 m (Table 4), but variation between blocks was high (Fig. S1 in Supplementary material). A detailed view of between-block and between-mountain variation in decomposition rates is given in Fig. S1.

4. Discussion

Litter mas loss rates in our field mesocosms depended on both environmental conditions (foremost temperature) and biotic drivers (mesofauna, and meso- and macrofauna) of decomposition. Even with the high variation in decomposition rates attributed to small scale (i.e., between blocks) and larger scale (i.e., between mountains) heterogeneity, and even though the mean temperature difference between 600 m and 1200 m during the experiment was only 1.8 °C, it was possible to identify altitudinal (as proxy for temperature effects) and fauna effects as drivers of differences in decomposition rates. The effects, however, depended strongly on the litter quality.

Despite our efforts to simulate a difference of 3.6 °C, the observed difference between the 600 and 1200 m a.s.l. sites was smaller than the predicted by the "rule of thumb" of −0.6 °C per 100 m, and smaller than observed in the 60's and 70's in mountains of Germany and Austria (Green and Harding, 1980). For the period July–September 1967–1971 in West Germany, the air adiabatic rate was about −0.7 °C per 100 m (Green and Harding, 1980). In the same months in 1974 in Austria, the soil adiabatic rate (20 and 30 cm) was 0.55–0.75 °C (Green and Harding, 1980). Adiabatic rates are expected to decrease due to an intensification of warming with elevation (Kotlarski et al., 2012). Indeed, in the European Alps, temperatures have already increased by about 0.35 °C per decade from 1959 to 2008 (Ceppi et al., 2012).

Regardless of fauna and altitude, the decomposition rate of high-quality litter was ~200% higher than that of the low-quality under field conditions. The marked importance of litter quality driving decomposition rates, however, was expected (Trofymow et al., 2002). Litter decomposition rates are usually positively correlated with the initial N content (Melillo et al., 1982; Zhang et al., 2008), which was much higher in *Urtica* (3.6%) than in hay (1.7%). In a meta-analysis of 70 litterbag studies, latitude (acting as a proxy for mean annual temperatures) and litter quality traits (C:N, total N) were found to be the major co-factors regulating litter decomposition rates in the field, but litter quality alone explained the largest part of variability (Zhang et al., 2008). Our high-quality litter, *Urtica dioica*, is a perennial nitrophilic weed (Rosnitschek-Schimmel, 1985) whose leaves are rich in nitrogen and poor in lignin (Lehtomäki et al., 2008). The addition of *Urtica* litter to the soil is usually beneficial to its fertility as it tends to increase N pools and nitrate-N leaching (Scheu, 1997), as well as microbial P, C, and N, and ergosterol (a proxy for fungal biomass) (Khan and Joergensen, 2006). On the contrary, hay and grass litter in general are poor in N and very rich in lignin (Lehtomäki et al., 2008) and other phenolic compounds.

With respect to the effect of the soil fauna on decomposition rates we had two predictions: it would be (1) higher on high-quality litter, and (2) higher at the lower altitude (= higher average temperature). These predictions were partially met, as there was a clear indication

Table 2
Mixed-effect models explaining the variation in mass loss of high- and low-quality litter. Fixed factors were altitude (2 levels) and fauna (3 levels). Random factors included the effects of blocks nested within sites. The * indicates that the model deviance is statistically lower than the previous one (after a likelihood test). The low-quality litter data were log-transformed prior the analysis.

	Factor(s)	High-quality litter			Low-quality litter		
		AIC (model)	Deviance (model)	% of total variance	AIC (model)	Deviance (model)	% of total variance
Null model	Random (sites:blocks)	1221.0	1215.0	33%	−230.9	−236.9	64%
Model 1	Fixed (altitude) Random (sites:blocks)	1213.3	1205.3*	10% 23%	**−242.8**	**−250.8***	**19%** **45%**
Model 2	Fixed (fauna) Random (sites:blocks)	1139.9	1129.9*	26% 45%	−230.2	−240.2	1% 64%
Model 3	Fixed (altitude + fauna) Random (sites:blocks)	**1132.2**	**1120.2***	**35%** **36%**	−242.2	−254.2*	19% 45%
Model 4	Fixed (altitude x fauna) Random (sites:blocks)	1132.5	1116.5	36% 36%	−239.7	−255.7	20% 46%

Table 3
Estimated coefficients for the fixed factors of linear mixed models explaining the variation in litter decomposition rates (mg day^{-1}) depending on altitude and fauna. According to the model selection shown in Table 2 the effects of altitude and fauna treatment were significant for the high-quality litter, whereas for the low-quality only altitude was significant. Note that the coefficients of the low-quality litter are in the log-scale.

High-quality litter			
Fixed factor:level	Estimate	S. e.	P
Altitude: 600 Fauna: Macro + mesofauna	112.367	2.161	< 0.001
Altitude: 1200	9.085	2.778	0.002
Fauna: Mesofauna	−8.547	1.562	< 0.001
Fauna: Controls	−18.087	1.562	< 0.001
Low-quality litter			
Altitude: 600	3.74111	0.020	< 0.001
Altitude: 1200	−0.11458	0.028	< 0.001

that the soil fauna increased the decomposition of the high-quality litter, but this effect was similar at both altitudes. Our results confirm the trends seen in previous studies, where the soil fauna has a higher effect on high-quality litter (Hoover and Crossley, 1995; Rouifed et al., 2010). The high N content, combined with low phenolic content and low toughness of the high-quality litter makes it very palatable to detritivores, which are known to prefer litter with such traits (Zimmer, 2002; Quadros et al., 2014). Our second prediction was based on previous findings for similar altitudinal ranges showing that fauna effects on decomposition decrease with altitude, which could be attributed to a known decrease of abundance and/or richness with altitude (Wang et al., 2009). For instance, the percentage of total decomposition due to the presence of soil fauna was 37% at 500 m a.s.l. (evergreen broadleaf forest) and only 8% at 2150 m a.s.l. (alpine meadow), but at each altitude the litter decomposed faster when the fauna had access to it (Wang et al., 2009). Although data on macrofauna richness and abundance in our study sites is scarce, our own observations (J. Berg and M. Zimmer, unpubl. data) indicated that macrodetritivores (mainly isopods and diplopods) abundance decreases with altitude, they are uncommon around 1200 m a.s.l and almost lacking above 1800 m a.s.l. (A. Mahringer and M. Zimmer, unpubl. data). Nonetheless, there was only a small influence of altitude on the faunal effect. A simple explanation would be the lack of substantial differences of detritivore diversity and/or activity between the two altitudes. Also, it must be noted that our field experiments were done in summer when there were favourable conditions for the activity of soil invertebrates at both altitudes. Another explanation is that the detritivore assemblages of the two altitudes could have differed in richness and/or abundance but were equally efficient in the processing of high-quality litter, but this needs

Table 4
Leaf litter mass loss (mg day^{-1} ± s. e.) of high-quality (*Urtica dioica*) and low-quality (hay) litter at 600 and 1200 m a.s.l. in five mountains in Salzburg, Austria, during the growing season (July–September). Values within brackets are mass loss rates expressed in mg g^{-1} day^{-1} ± s. e. Different letters indicate statistically significant differences ($\alpha = 0.05$) between mountains after a one-way Analysis of Variance.

	High-quality litter		Low-quality litter	
	600 m	1200 m	600 m	1200 m
Gaisberg	93.49 ± 3.28 a (18.5 ± 0.6)	120.38 ± 0.60 a (23.7 ± 0.1)	37.62 ± 0.54 a (7.4 ± 0.1)	32.31 ± 0.69 a (6.3 ± 0.1)
Kleiner Göll	113.65 ± 4.23 bc (22.5 ± 0.8)	117.96 ± 2.97 a (23.3 ± 0.6)	44.04 ± 1.28 b (8.7 ± 0.2)	43.27 ± 0.92 b (8.5 ± 0.2)
Tristkopf	102.24 ± 2.21 b (20.3 ± 0.4)	97.96 ± 2.99 b (19.4 ± 0.6)	42.48 ± 1.50 b (8.4 ± 0.3)	34.77 ± 0.71 a (6.9 ± 0.1)
Untersberg	95.07 ± 3.48 ab (18.8 ± 0.7)	114.49 ± 2.53 a (22.7 ± 0.5)	45.29 ± 1.02 b (8.9 ± 0.2)	40.27 ± 0.38 c (7.9 ± 0.1)
Wirreck	112.99 ± 2.96 bc (22.3 ± 0.6)	112.07 ± 3.14 a (22.1 ± 0.6)	42.73 ± 0.75 b (8.5 ± 0.1)	38.67 ± 1.02 c (7.7 ± 0.2)

further testing with a clear focus on trait-based (rather than taxonomic) analysis.

We expected that decomposition would be faster at the lower altitude (higher average temperature), due to the known sensitivity of decomposition to temperature (Fierer et al., 2005). Our prediction was partially met because the negative relationship between altitude and decomposition rates was only seen in the low-quality litter. One explanation for the higher decomposition of the high-quality litter at 1200 m a.s.l. might be due to its very high N content. With increasing altitude there was an increase in abundance of beech and spruce at our field sites, which are species with leaf/needle litter poor in N and with high C:N ratio (Vesterdal et al., 2008). Thus, at 1200 m a.s.l., high-quality litter is a scarce resource for detritivore/decomposer communities, and the nettle offered in our mesocosms was a "hotspot of N". At the lower altitude, on the other hand, the presence of a more diverse vegetation (i.e. more options of resources) might have diluted this effect. Lower decomposition rates at higher altitudes have been observed for different litter qualities (high vs. low), or fractions of the same litter (labile vs. recalcitrant) (Shanks and Olson, 1961; Coûteaux et al., 2002). Shanks and Olson (1961) found an increase of 4.8% of mass loss for each 610 m decrease in altitude in the range of 260–1600 m a.s.l., both for a relatively high-quality (mulberry) and low-quality litter of *Fagus sylvatica* (beech). In another latitudinal gradient, from 500 to 2150 m a.s.l. in humid forests, decomposition rates decreased with altitude, and the relatively high-quality litter decomposed faster than the low-quality one as well (Wang et al., 2010). Other studies with altitudinal gradients have confirmed the expectations that decomposition rates of low-quality are more sensitive to temperature (Leifeld and Fuhrer, 2005). Along a gradient from 65 to 3968 m a.s.l., the labile fraction of wheat straw decomposed faster than the recalcitrant one, irrespectively of altitude, and the recalcitrant fraction decomposed slower with increasing altitude (Coûteaux et al., 2002).

Differences in litter quality have an important role in the decomposition process and must be taken into account when predicting soil-climate feedbacks and the dynamics of soil organic carbon stocks (Cornelissen et al., 2007). Litter quality controls the sensitivity of decomposition to temperature (Leifeld and Fuhrer, 2005; Fierer et al., 2005), as shown here, and also the amount of CO_2 that is produced during decomposition versus the fraction of the litter that is sequestered in the soil as recalcitrant organic matter. The metabolic quotient in the litter layer – a measure of microbial respiration per unit of biomass C – is positively correlated with the litter C:N ratio and negatively correlated with litter N (Spohn, 2015). Thus, the proportion of carbon respired per unit of decomposer biomass is negatively correlated with litter quality (Spohn, 2015). For instance, upon the decomposition of *Urtica* and beech litter added to the soil, the CO_2 production on beech was 34.8% of the carbon added, while for *Urtica* it was only 20.1% (Scheu, 1997). Therefore, upon temperature increase, not only will the low-quality litter be more affected but also the CO_2 produced during the process will increase. These effects, however, will not be accompanied by an increase in mineralization of important nutrients and positive feedback to plants, due to the low quantities of N, P, K, and Ca usually observed in low-quality litters. Considering that the vegetation of our study sites, and of many forests of Central and Northern Europe, are composed mainly of *F. sylvatica* and conifers, which are examples of species producing slow-decomposing, recalcitrant litter (Vesterdal et al., 2008), our results indicate that decomposition in these regions will not only proceed faster upon predicted warming but also produce more CO_2 (Spohn, 2015).

The observed soil organic carbon stocks of today were formed under the dynamics of litter input and its decomposition rates, mediated by litter quality (Cotrufo et al., 2013). Therefore, changes in either component will influence the stability of current soil organic stocks and how future ones will form. It is already known that the litter production of broadleaf forests of Eurasia is sensitive to increase in temperature (Liu et al., 2004), and it is necessary to understand the dynamics of soil organic matter as well. Studies of the effects of climate change on soil processes should be carried on field conditions more often, in order to produce more realistic results, and the use of altitudinal gradients in a space-for-time approach provides a useful way of achieving that. For instance, the mean annual temperature is predicted to increase by about 1.6 °C in the next 33 years in Austria (Strauss et al., 2013), and we were able to detect an increase of 12% in decomposition rates with an increase in 1.8 °C in temperature.

To conclude, the use of the Space-for-Time approach proved to be extremely useful to detect the interacting effects of temperature, litter quality, soil fauna and microorganisms on litter decomposition rates in the field. Moreover, the use of SFT coupled to a proper spatial replication allowed us to detect, and account for, a large variability due to spatial heterogeneity in moisture, slope inclination, soil depth, vegetation cover and insolation, etc. According to our results, the mesofauna and macrofauna were not significant players on the low-quality litter decomposition, at least when high-quality litter was available in the vicinity of few decimeters. Climate-induced changes in detritivore communities might have minor effects on decomposition rates in forest ecosystems where most of the litter is of relative low-quality. It is clear from our results, and many previous studies, that the effects of climate change on litter decomposition cannot be generalized and that litter quality must be taken into account. The composition of the vegetation, as an indicator of the quality of the litter that is produced, must be explicitly included in models, as the consequences of increased temperature will not be the same for all litter types. If forest management is to be used as a solution to mitigate the effects of climate change, the quality of the litter produced must be taken into account when choosing the plant species to be used. The sensitivity of the low-quality litter decomposition to a small temperature increase (∿1.8 °C) seen in our study, coupled to the expected relative increased CO_2 respired during the process (Spohn, 2015) supports the idea that Northern temperate forests may to need N fertilization to counteract the negative effects of warming on the decomposition rates of low quality litter, i.e., increased CO_2 emissions (Prescott, 2010).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2018.05.010.

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